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The development of the megagametophyte of Ailanthus altissima.

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THE DEVELOPMENT OF THE MEGAGAMETOPHYTE OF *AILANTHUS ALTISSIMA*

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The Development of the Megagametophyte of *Ailanthus Altissima*

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C H A P T E R I

INTRODUCTION

A conception of the orderly and logical process of the development of the ovule is of primary importance to the student of botany. Descriptions of the construction and organization of the plant body are needed to solve functional aspects of plant development and to trace underlying similarities in form between various plants.

Comparison of the flower parts and structures connected with sexual reproduction is one of the most dependable and most frequently used bases for judgment as to the relationship of plants. Reproductive structures are more dependable than vegetative organs as indicators of relationships. They are shorter-lived and are subjected for shorter periods to environmental influences. Their relation to the environment is not so close and their structure is less likely to vary in response to changes in the environment.

On account of this greater stability of reproductive structures and relatively greater value in showing actual relationships, morphological studies of the development of flower parts have been of prime importance in classification.

Recent botanical research indicates a trend of increased interest in the morphological development of plants. Numerous detailed studies of the early development of the ovule, megasporogenesis and the development of the megagametophyte are recorded in recent botanical literature. The greater number of these studies have been made in the family Leguminosae. No studies concerning the development of the ovule of Ailanthus altissima have been made.

It is the purpose of this study to trace the development of the megagametophyte in Ailanthus altissima.

C H A P T E R II

MATERIALS AND METHODS

Pistillate panicles of Ailanthus altissima Swingle were collected at two day intervals beginning May 26, 1942 through July 22, 1942. These were collected from mature trees on Poplar Level Road near Louisville, Kentucky. Since the flowers in a panicle do not open at the same time, varying degrees of development were found in each pistillate panicle.

Flowers were dissected to observe the number and arrangement of flower parts. Measurements of the spread of the petals and the length of the samaras were recorded. The length of the flowering period was recorded.

The panicles were fixed in formalin acetic alcohol, as given by Chamberlin (1932). The buds and flowers were dissected and the five deeply cleft ovaries dehydrated by the Zirkle (1930) method and embedded in paraffin.

Serial sections were cut ten microns in thickness. They were stained with gentian violet and mounted in balsam.

Camera-lucida drawings were made at table level.

C H A P T E R III

DESCRIPTION OF FLOWER PARTS

The greenish-white polygamo-dioecious flowers of Ailanthus altissima are borne in terminal upright panicles 10 to 20 cm. long. The average number of potential flowers present in a pistillate panicle for three consecutive years was 146 flowers. The counts were made at the time the first flowers were opening, so all buds were considered potential flowers.[1]

The flowers in a panicle do not all open at the same time. The average period from the beginning to the end of flowering in pistillate panicles was 10 days, from June 2 through June 12. Table I shows that the average percentage of flowers open June 2 was 20.1; for June 5, 20.0; for June 8, 51.1; for June 10, 53.7 and for June 12, 6.7. This data is included as a basis for determining the opening of the first pistillate flowers.

Table II shows the increase in length of the buds from May 26 to June 2. The average for 25 bud lengths shows a gradual increase in size from 2.61 mm. on May 26 to 4.24 mm. on June 2.

The flowers are small and usually regular

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[1] Unpublished data by P. A. Davies

with five spreading, valvate, greenish-white petals. The average of 500 measurements of the spread of petals of pistillate flowers was 6.9 mm.[2] The petals are several times longer than the five imbricated sepals and are inserted on a ten-lobed flattened disc. Pistillate flowers have a gynoecium of five united carpels. The pistil contains a five-lobed flattened ovary, with a solitary ovule in each cavity. The ovule becomes anatropous as it develops. The styles are united, twisted rope-like and have elongated spreading stigmas. Ten non-functional stamens are inserted at the base of the disc.

The fruit, an elongated samara, has a membranous, veiny wing and a single, compressed seed is situated in the middle.

Table III shows the average length of 25 fruits in panicles collected from June 2 through July 1. The data indicates an increase from 2.5 mm for fruits in panicles collected June 2 to 38.9 mm for fruits collected July 1. Widely varying degrees of fruit development were found in each panicle.

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[2] Ibid., p. 5.

TABLE I. FLOWERING PERIOD OF AILANTHUS ALTISSIMA

Date		Number of buds and flowers per panicle										Per cent Buds open
		1	2	3	4	5	6	7	8	9	10	
May 30	Buds	173	108	167	108	114	167	150	161	167	138	0
	Flowers	0	0	0	0	0	0	0	0	0	0	
June 2	Buds	164	125	173	157	70	157	196	157	235	102	20.1
	Flowers	47	22	39	39	16	55	16	0	39	39	
June 5	Buds	152	221	233	132	172	104	60	72	160	152	20.0
	Flowers	52	80	16	8	0	28	8	20	40	40	
June 8	Buds	138	167	161	150	167	114	108	167	108	173	51.1
	Flowers	78	72	102	54	114	78	72	71	42	60	
June 10	Buds	116	136	194	168	174	103	132	149	187	110	53.7
	Flowers	0	52	97	110	84	70	123	123	58	67	
June 12	Buds	120	106	134	197	106	176	268	127	134	92	6.7
	Flowers	0	0	7	7	21	28	21	7	7	0	
June 14	Buds	110	149	187	123	103	168	174	116	194	136	0
	Flowers	0	0	0	0	0	0	0	0	0	0	

TABLE II. GROWTH OF BUDS

Measurements of Buds in mm.			
May 26	May 28	May 30	June 2
2.50mm.	3.00mm.	3.50mm.	4.25mm.
2.25	2.90	3.25	5.00
3.00	2.95	2.90	4.25
2.75	2.85	3.60	4.75
3.10	3.30	3.75	4.05
2.90	2.85	4.00	4.00
2.80	2.80	3.95	4.30
2.75	3.10	3.50	4.40
2.80	2.85	3.55	4.50
2.75	2.75	2.50	4.10
2.40	2.85	3.75	4.25
2.50	2.95	3.25	4.05
2.60	2.75	3.15	3.75
2.50	2.75	2.75	4.35
2.00	2.80	3.05	4.75
2.60	2.50	3.25	4.05
2.05	2.55	4.00	4.80
2.25	2.90	3.75	3.60
3.00	2.90	3.80	3.25
2.55	2.95	3.35	4.50
2.85	2.00	3.25	4.35
2.45	2.75	3.60	4.25
2.90	2.70	3.00	4.50
2.80	2.90	3.20	4.55
2.50	2.80	3.35	3.50
Average 2.61mm.	2.81mm.	3.28mm.	4.24mm.

TABLE III. GROWTH OF FRUITS OF AILANTHUS ALTISSIMA

Measurements of fruits June 2 - July 1 in mm.												
J'2	5	8	10	12	14	16	18	20	23	26	28	Ju.1
2.4	2.9	5.2	6.5	5.5	10.0	10.0	17.5	18.0	16.5	25.0	21.0	41.0
2.5	2.8	5.2	7.5	5.0	9.0	8.0	9.5	18.5	23.0	30.5	23.0	34.0
2.3	3.0	4.6	7.0	5.5	8.5	6.5	9.0	17.0	24.0	26.0	28.5	39.0
2.6	3.1	5.3	5.0	7.5	8.0	9.0	9.0	18.0	27.0	29.0	29.0	40.0
2.5	3.1	5.5	6.0	6.0	10.0	6.5	10.0	12.5	25.0	23.5	27.0	41.0
2.7	2.7	4.5	6.5	4.5	9.0	11.0	14.5	14.0	25.0	24.5	28.5	38.0
3.0	2.9	4.7	6.5	5.0	8.5	9.5	14.0	13.5	18.0	27.0	30.0	35.0
2.7	3.0	4.6	5.0	7.0	8.0	10.0	14.5	19.0	17.5	22.0	28.5	40.0
2.2	2.8	5.1	6.5	8.0	9.0	9.5	12.0	18.0	25.5	27.0	28.0	41.0
2.2	2.9	4.2	4.5	8.0	6.5	10.5	12.5	17.0	19.0	32.0	26.0	34.0
2.6	2.9	4.4	8.0	7.5	6.5	6.0	13.0	12.0	16.5	26.0	25.0	39.0
2.2	3.0	4.0	8.0	5.0	10.0	14.5	17.0	17.0	27.0	30.0	30.0	39.0
2.2	2.9	4.2	8.0	6.5	9.0	9.0	15.0	18.5	18.0	23.0	27.0	37.0
2.0	2.3	4.2	6.5	6.0	8.0	9.0	14.5	16.0	19.0	26.0	28.5	41.5
2.7	2.3	4.1	5.0	7.0	6.5	10.0	13.5	19.0	18.5	27.0	32.0	36.0
2.5	2.6	4.2	7.0	6.5	7.5	11.5	15.0	15.0	17.5	22.0	27.0	39.0
2.5	2.7	4.2	6.5	7.0	8.5	11.0	12.0	14.5	18.0	28.0	27.0	42.0
2.4	3.0	4.0	4.0	5.5	8.0	9.5	11.0	13.0	21.0	29.0	30.0	38.5
2.3	2.7	4.7	4.7	6.5	8.0	9.0	12.0	18.0	21.5	24.0	26.5	49.0
2.3	2.5	4.0	5.2	6.5	7.5	10.0	6.0	17.0	20.0	22.0	27.0	43.0
2.4	2.6	4.6	4.0	7.0	9.5	10.0	6.5	15.0	14.0	23.0	27.0	35.0
2.4	2.3	4.4	7.0	5.5	10.5	10.5	10.0	11.0	20.5	28.0	24.0	34.5
2.6	2.5	4.4	4.0	5.5	8.0	6.0	11.0	12.0	16.0	28.0	26.0	34.0
2.7	3.0	4.5	6.5	9.0	9.0	8.0	9.5	15.0	17.5	21.0	28.5	40.0
Average 2.5	2.8	4.6	5.8	6.3	8.3	9.2	11.9	15.9	19.9	25.9	27.4	38.9

CHAPTER IV

DEVELOPMENT OF THE OVULE

A solitary ovule arises in each carpel of the five-lobed flattened ovary. The young ovule is initiated by the multiplication of the hypodermal cells of the placenta (Plates I and II). As the rounded protuberance of undifferentiated cells pushes out into the carpel of the ovary and continues to develop, cell division becomes more active on one side with the result that the ovule begins to bend toward the apex of the ovary (Plate III). Weinstein (1926), in Phaseolus found a similar curvature of the ovules toward the apex of the ovary.

The curvature of the ovule begins before the ovule touches the dorsal wall of the ovary. D. C. Cooper (1933, 1942), in Melilotus alba and Lobelia cardinalis, and G. O. Cooper (1941), in Phryma leptostachya found that the continued growth and elongation of the funiculus and more rapid division of the cells in the chalazal region of the ovule opposite the placenta cause the ovule to curve inward toward the base of the ovule. Reeves (1930), in his study of the ovule of Medicago sativa, concluded that the direction of this curvature may be determined mechanically by the growth of the carpel.

He found that the young ovule of Medicago sativa was orthotropous until it came in contact with the dorsal wall of the ovary and then it began to bend, usually toward the base. Reeves observed that occasionally, owing to the pressure exerted by the carpel wall, one of the upper ovules curved toward the stylar end.

No sharply differentiated archesporial cell could be found (Plates I. II, and III). It was difficult to determine whether a cell was sporogenous until after the archesporial cell divided. The same situation was found by Reeves (1930), in Medicago sativa. A single archesporial cell which can easily be identified by its dense cytoplasm and large nucleus is the usual case in angiosperms. Most observers of the Leguminosae have found a differentiated archesporial cell. G. O. Cooper (1941, 1942a, 1942b), in Phryma leptostachya, Lobelia cardinalis, and Plantago lanceolata found that an apical hypodermal cell was early differentiated as a primary archesporial cell. He found that this cell had denser cytoplasm and a somewhat larger nucleus than the remaining cells of the ovary.

Cases of multiple archesporium have been reported by Strasburger (1880), in Rosa, Chamberlain

(1897), in Salix, Conrad (1900), in Quercus, Murbeck (1901), in Alchemilla, Lloyd (1902), in Callipeltis, Martin (1914), in Trifolium and Medicago sativa, Reeves (1930), in Medicago sativa and D. C. Cooper (1935), in Medicago. In Medicago sativa, Martin (1914), reported that the number of archesporial cells ranged from one to six and that more than one usually occurs. Martin found two to four rows of megaspores in the same nucellus and found that often more than one megaspore starts to form an embryo sac, but not more than one matures.

As the ovule continues to develop the cells of the nucellus become aligned or organized about the potential archesporial cell, which is not differentiated at this early stage of development (Plate III).

An inner integument, usually of two layers of cells, except at the base where it occasionally had three layers of cells, develops as a meristematic outgrowth from the chalazal cells below the potential archesporial cell. It grows upward about the apex of the nucellus. As the integument forms, there is more rapid growth of the ovule on the side away from the main axis. As growth continues, the ovule bends upward and toward the apex of the ovary (Plates III and V).

Later, the outer integument, usually of three layers of cells, develops from the nucellus at a level just below the inner integument. The outer integument grows more rapidly on that side of the ovule away from the placenta and shows little development on the side toward the placenta (Plate IV).

The two layers of the inner integument grow more rapidly than the outer integument, surround the ovule and become more massive in the micropylar region. A similar development of the inner integument was found by D. C. Cooper (1940), in Portulaca oleracea and Andersen (1927), in Poa pratensis and Poa compressa. The outer integument never reaches beyond the level of the apex of the nucellus. This condition is like that found by D. C. Cooper (1940), in Portulaca oleracea, in which he found that the outer integument arose as a meristematic outgrowth of the epidermis of the ovule just basal to that of the inner integument. The outer integument grew more slowly; so that it never reached a point where its apex took any part in the formation of the micropyle. Contrary to this type of development of the integuments, D. C. Cooper (1933), in Melilotus, described an outer integument which grew more rapidly than the inner and became massive at the region of the micropyle. The inner integument

was only two layers in thickness and grew over the apical end of the embryo sac so as to leave a very short inner portion of the micropyle.

The curvature of the ovule in Ailanthus continues until the longitudinal axis is approximately parallel with that of the ovary wall to which it is attached. The ovule becomes typically anatropous by the time the embryo sac is mature (Plate V). Similar curvature of the ovule is described by G. O. Cooper (1942a, 1942b), in Lobelia cardinalis and Plantago lanceolata.

The main vascular strand extends into the base of the funiculus. A group of nutritive cells having very dense cytoplasmic content is found about the chalazal end of the developing megagametophyte (Plates VII, VIII and XI).

CHAPTER V

MEGASPOROGENESIS AND THE DEVELOPMENT OF THE MEGAGAMETOPHYTE

The archesporial cell which is deeply embedded in the nucellus functions as the megaspore mother cell, increases in size and through two divisions gives rise to a linear tetrad of megaspores (Plates IV and VI).

In Medicago sativa, Reeves (1930), found that the archesporial cell did not directly function as the megaspore mother cell. It first divided and gave rise to a primary parietal cell and a primary sporogenous cell. He found that tranverse divisions of the parietal cell occurred and gave rise to the three parietal layers, the cells of which might divide again. As a result of this procedure, the sporogenous tissue was deeply embedded. Also he found that the primary sporogenous cell was conspicuous because of its greater size and its enlarged nucleus. Reeves found that the primary sporogenous cell developed directly into the megaspore mother cell without dividing again and by two meiotic divisions gave rise to a tetrad of megaspores.

While a linear row of four megaspores is the usual case in the Leguminosae, variations in

the number of megaspores and their arrangement have been observed. Guignard (1881), noted the formation of only three in Phaseolus multiflorus and in Medicago arborea. Weinstein (1926), found the presence of three to be typical of Phaseolus vulgaris. Weinstein believed this to be brought about as the result of an abortive homotypic division of the micropylar cell.

Reeves (1930), in Medicago sativa, found instead of an axial row of four spores, resulting from two horizontal meiotic divisions, as is typical, the first division of the megaspore mother cell is at right angles to the long axis of the nucellus and the plane of the second division sometimes longitudinal. The latter condition was found occasionally in the terminal member of the diad. Mottier (1895), in Ranunculus and Baranov (1926), in Drimopsis maculata, also discovered this unusual type of tetrad arrangement. Duncamp (1902) reported various groupings of megaspores in tetrads of Fatsia japonica.

Young (1905), in Melilotus alba, reported that the megaspore mother cell developed into the embryo sac without first undergoing tetrad division. Coe and Martin (1920), in their investigation of Melilotus alba, showed that a first division of the megaspore mother cell did occur and that it resulted

in the formation of two daughter cells with the inner megaspore the one that persists.

Reeves (1930), in Medicago sativa, has shown that two or three tetrads are often found, but that only a single megaspore has ever been found to develop into a mature embryo sac. In extreme cases, Reeves found that the chalazal megaspore of as many as three tetrads persist and undergo first stages of development, but that two of these megaspores disappear about the time of the two-nucleate stage.

In Ailanthus altissima, the chalazal spore is the largest of the four megaspores. This chalazal spore alone develops into the embryo sac and the other megaspores disintegrate (Plates VI and VII). This condition has been noted by Martin (1914), Reeves (1930), G. O. Cooper (1942), and D. C. Cooper (1940), in various species studied. Their studies have shown that the chalazal megaspore of the row of three or four became the functional embryo sac mother cell and that the other spores disintegrated.

Unlike this type of development, Guignard (1881) in Medicago arborea, found the lily type of embryo sac development in which all four megaspore nuclei participate in the formation of the embryo sac. Early investigation of Medicago and closely

related genera of Leguminosae indicated that megasporogenesis proceeded as in Lilium and all four megaspores function. Herail (1889) in Medicago arborea and Young (1905) in Melilotus alba were in agreement with Guignard.

More recent investigations by Martin (1914) in Medicago sativa and Vicia americana, Coe and Martin (1920) in Melilotus alba, Reeves (1930) and D. C. Cooper (1935) in Medicago sativa have reported that the process is the same as that usually found in the dicotyledons in which one of the megaspores only is functional while the other three disintegrate.

Shattuck (1905) has reported that the Lilium or Adoxa type of development occurs in the majority of cases in Ulmus americana. Stenar (1927) described a modification of the Adoxa type in Gagea, in which the megaspore mother cell undergoes two divisions, forming a linear row of four megaspore nuclei, without the intervention of cell walls. All four nuclei divide again, forming a typical eight-nucleate megagametophyte or only the three nuclei nearest the micropyle divide and the chalazal nucleus degenerates. Dahlgren (1916) in Armeria and Statice, Haupt (1934) in Plumbago capensis and Walker (1938) in Ulmus fulva have reported that all four megaspore nuclei enter

into the development of the megagametophyte.

In Ailanthus altissima, the megaspore toward the chalazal end becomes the functional megaspore (Plate IV). Variations as to the position of the functional megaspore have been observed. Guignard (1881) found that the third megaspore from the micropylar end of the tetrad functions in several species of Acacia and Saxton (1907) found a similar situation in Cassia tomentosa. In several ovules of Poa pratensis and Poa compressa, Andersen (1927) found that the outermost megaspore developed and formed the embryo sac.

The persisting chalazal megaspore in Ailanthus altissima increases in size and its nucleus divides mitotically in the typical way (Plates IV and VI). The two nuclei migrate apart and lie in a peripheral layer of cytoplasm in the micropylar and chalazal ends of the cell (Plates VII and VIII). Before these daughter nuclei divide again, the embryo sac becomes greatly elongated and a large vacuole occupies the mid-portion of the cell. The increase in diameter of this cell is somewhat greater in the apical portion of the embryo sac (Plate XI).

As a result of two further divisions, a typical eight-nucleate megagametophyte is formed (Plates IX

and XI). The nuclei in the chalazal end become separated from the remainder of the embryo sac and each lies in an individual mass of cytoplasm, forming three uninucleate antipodal cells. The three nuclei at the micropylar end, two synergids and the egg nucleus, become the egg apparatus. The egg nucleus is larger than the nuclei of the synergids and lies in a mass of cytoplasm within the embryo sac. The two nuclei devoid of a limiting membrane become polar nuclei. One of these from the chalazal and one from the micropylar end of the cell migrate to the center of the cell and lie in close contact to each other (Plates X and XI).

Guignard (1881) made the earliest detailed study of the embryo sacs of a number of the Leguminosae. More recent studies by Reeves (1930) in Medicago, D. C. Cooper (1935, 1938, 1940) in Medicago, Pisum sativum, and Portulaca oleracea; and by G. O. Cooper (1942a, 1942b) in Lobelia cardinalis and in Plantago lanceolata report the formation of typical eight-nucleate seven-celled megagametophytes.

Variations from the typical formation of three, uninucleate antipodal cells in embryo sacs have been reported. Johannsen's work (1884) on Hordeum showed an increase in the number to thirty-six

or more antipodals before fertilization and disorganization of these cells with the beginning of endosperm development. Koernicke (1896) in Triticum and Cannon (1900) in Avena fatua found a similar increase in the number of antipodals. Afzelius (1924) in his study of Senecio found the antipodals of the forms he examined to be either binucleate or multinucleate. He stated that in some instances antipodals may divide so that instead of having three antipodals a large number may be present. Reeves (1930) in Medicago sativa found that occasionally only one nuclear division occurred in the chalazal end and six instead of eight nuclei were formed in the embryo sac. Walker (1938) in Ulmus fulva stated that occasionally four antipodals were present.

The egg apparatus of Ailanthus altissima is similar to that described by Reeves (1930) in Medicago sativa, Walker (1938) in Ulmus fulva, D. C. Cooper (1940) in Portulaca, and G. O. Cooper (1942a) in Lobelia cardinalis, in that the egg cell is the largest of the three cells and has a much larger nucleus than the synergids which elongate and extend toward the micropyle.

The two polar nuclei in Ailanthus fuse shortly after the formation of the megagametophyte before

fertilization to form a primary endosperm nucleus (Plate XII).

D. C. Cooper (1933, 1935) in Melilotus and Portulaca, Walker (1938) in Ulmus, and G. O. Cooper (1942a) in Lobelia found that the polar nuclei fused to form the primary endosperm nucleus before fertilization.

Mendes (1941) in Coffea arabica reported that the embryo sac ready for fertilization may show the polar nuclei fused or separate. Fusion seemed to be accelerated by pollination. When pollination failed, he found that fusion did not occur but the embryo sac remained intact for a variable length of time.

Reeves (1930) in Medicago sativa stated that the polar nuclei did not completely unite until the time of fertilization. He observed stages in which the polar nuclei had begun to fuse before fertilization. Reeves believed this partial fusion a result of delayed fertilization. D. C. Cooper (1935) in Medicago and G. O. Cooper (1938) in Pisum found that the polar nuclei united at the time of fertilization.

In Ailanthus altissima, the embryo sac just prior to fertilization consists of the egg cell, the primary endosperm cell and three antipodal cells

which have separated from the remainder of the embryo sac. The synergids disintegrate early (Plate XII).

Weinstein (1926) found that both the antipodals and synergids of Phaseolus vulgaris disintegrated early and that at the time of fertilization the embryo sac consists of but two cells, the egg and the primary endosperm cell.

In species that have been examined, the time at which the antipodals disintegrate varies greatly. Unlike the condition found in Ailanthus, Reeves (1930) in Medicago, D. C. Cooper (1933, 1940) in Melilotus and Portulaca and G. O. Cooper (1941) in Phryma found that the antipodals disappeared very early before fertilization.

Andersen (1927) in Poa pratensis and Poa compressa has shown that the Gramineae are conspicuous for their strongly developed antipodals. The antipodals were found to increase in size in comparison to the egg and each contained a very large nucleus with several nucleoli. He found that the three very large antipodal cells persisted until late in endosperm formation, when they were finally crowded off to one side, digested and absorbed by the growing endosperm.

Small (1919) in his study of the Compositae recorded that the chalazal antipodal may divide to form as many as four cells, each having one or more nuclei. This elongated structure was spoken of as an aggressive haustorium. G. O. Cooper (1942a) reports that the antipodals of Lobelia cardinalis persisted, became enlarged and functioned as haustoria, and digested the cells of the nucellus.

Unlike the condition found in Ailanthus altissima in which the synergids disintegrate shortly after the formation of the mature megagametophyte, D. C. Cooper (1933) in Melilotus found that the synergids persisted until an embryo of some size was formed. The synergids were also found to persist after fertilication by G. O. Cooper (1941, 1942a, 1942b) in Phryma, Lobelia and Plantago. Mendes (1941) in Coffea arabica stated that the synergids disappeared at the passage of the pollen tube over the synergids.

The mature megagametophyte is surrounded by several layers of cells of the nucellus. The adjacent nucellar cells become elongated and are digested and absorbed by the embryo sac (Plates X and XI).

Reeves (1930) in Medicago sativa, D. C. Cooper (1935) in Medicago sativa, and G. O. Cooper (1942a,

1942b) in Lobelia cardinalis and Plantago lanceolata, observed that the nucellus at the micropylar end disappeared and the embryo sac came in contact with the integuments. The integument contained the reserve food. The only place in which the nucellus remained in contact with the megagametophyte was at the antipodal end.

In Ailanthus, the large nutritive cells of the nucellus at the chalazal end of the embryo sac have dense cytoplasmic content and large nuclei. They persist throughout the development of the megagametophyte (Plates X, XI, and XII).

Reeves (1930) found that the nutritive material for the embryo sac was derived chiefly from the digestion and absorption of the adjacent nucellar cells, and that partly specialized cells also served in the conduction of food to the embryo sac. These cells which have been described by Ernst (1910) in Tulipa gesneriana and by him termed "Leitzellen" were of striking appearance and extended into the chalazal end of the embryo sac. By the time the female gametophyte was mature, Reeves found that vessels could be traced from the base of the funiculus to the "Leitzellen".

In Ailanthus altissima there were no specialized

cells for the conduction of food from the vascular strand in the funiculus to the chalazal end of the female gametophyte.

C H A P T E R VI

SUMMARY

The greenish-white polygamo-dioecious flowers of Ailanthus altissima are borne in upright panicles.

Widely varying degrees of fruit development are found in each panicle.

The flowers are small, usually regular with five spreading valvate greenish-white petals inserted on a ten-lobed flattened disc, five imbricated sepals and ten non-functional stamens inserted at the base of the disc.

The fruit, an elongated samara, has a membranous, veiny wing and a single, compressed seed is situated in the middle.

Pistillate flowers have a gynoecium of five united carpels. Each carpel of the five-loculed pistil contains a solitary ovule which is anatropous at maturity.

The archesporial cell which is deeply embedded in the nucellus is not sharply differentiated and could not be distinguished until after it divided.

An inner integument of two layers of cells develops more rapidly than the outer integument of three layers, surrounds the ovule, and becomes massive in the micropylar region. The outer integument never reaches beyond a level even with the apex of the nucellus.

The main vascular strand extends into the base of the funiculus. Nutritive cells of dense cytoplasmic content are found about the chalazal end of the megagametophyte.

A linear row of four megaspores is formed as a result of two divisions of the archesporial cell which functions as the megaspore mother cell.

The chalazal megaspore of the tetrad is the largest and becomes the functional embryo sac mother cell. The three micropylar megaspores disintegrate.

A typical eight-nucleate seven-celled megagametophyte is formed which consists of three antipodal cells at the chalazal end; three larger cells, the egg apparatus, at the micropylar end; and a large central two-nucleate endosperm cell. The polar nuclei fuse shortly after the formation of the megagametophyte.

The synergids extend into the micropylar end of the embryo sac and disintegrate before the antipodals at about the time the primary endosperm cell is formed.

The diameter of the megagametophyte becomes greatly extended during the course of development from the first nuclear division onward. The adjacent cells of the nucellus become flattened and elongated.

They disintegrate as the megagametophyte enlarges.

The micropylar end of the megagametophyte at maturity is surrounded by several layers of the nucellus.

C H A P T E R VII

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C H A P T E R VIII

PLATES

Key to Plates

anti.	--	antipodal cells
arch.	--	archesporial cell
carp.	--	carpel
chal.	--	chalazal
egg	--	egg cell
ex. teg.	--	external integument
funi.	--	funiculus
integ.	--	integument
in. teg.	--	inner integument
meg.	--	megagametophyte
micro.	--	micropylar
nuc.	--	nucellar cells
nucl.	--	nuclei
nutri.	--	nutritive cells
pol. nucl.	--	polar nuclei
pri. end.	--	primary endosperm
syn.	--	synergids
tetra.	--	tetraspores
vac.	--	vacuole
vas. st.	--	vascular strand

PLATE I

Early Development of the Ovule

PLATE I

Camera-lucida drawing of an early stage in the development of the ovule in a bud 2.61 mm. in length, (collected May 26) showing the formation of a rounded protuberance of undifferentiated nucellar cells in the cavity of the ovary. More rapid development appears on one side of the young ovule. 1530 diameters.

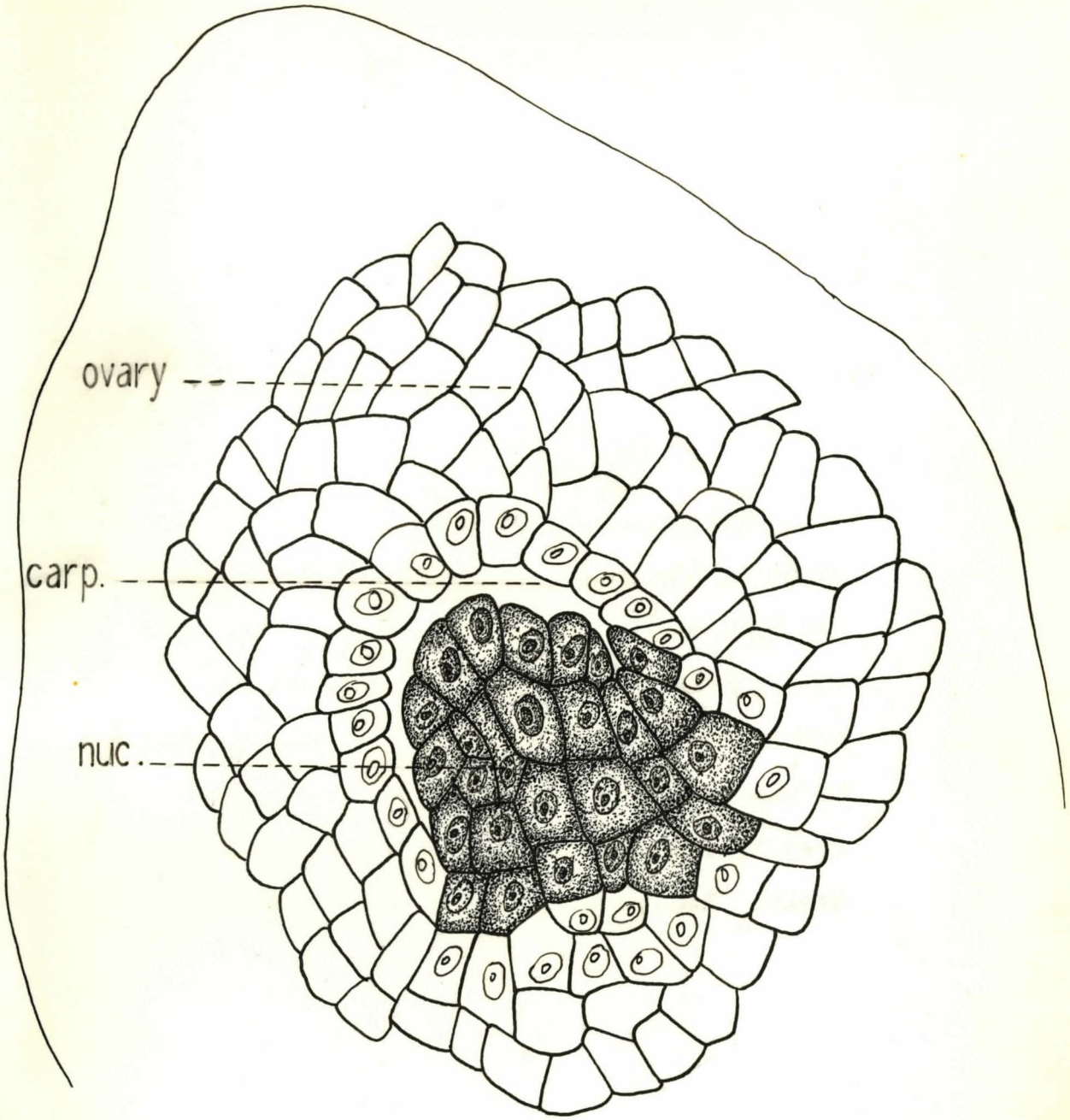

PLATE I.

PLATE II

Undifferentiated Archesporial Cell

PLATE II

Camera-lucida drawing of longitudinal section of the ovary in a bud 2.6 mm. long, (collected May 26) showing an alignment of the undifferentiated cells of the developing ovule. No archesporial cell can be distinguished at this stage of development. 1525 diameters.

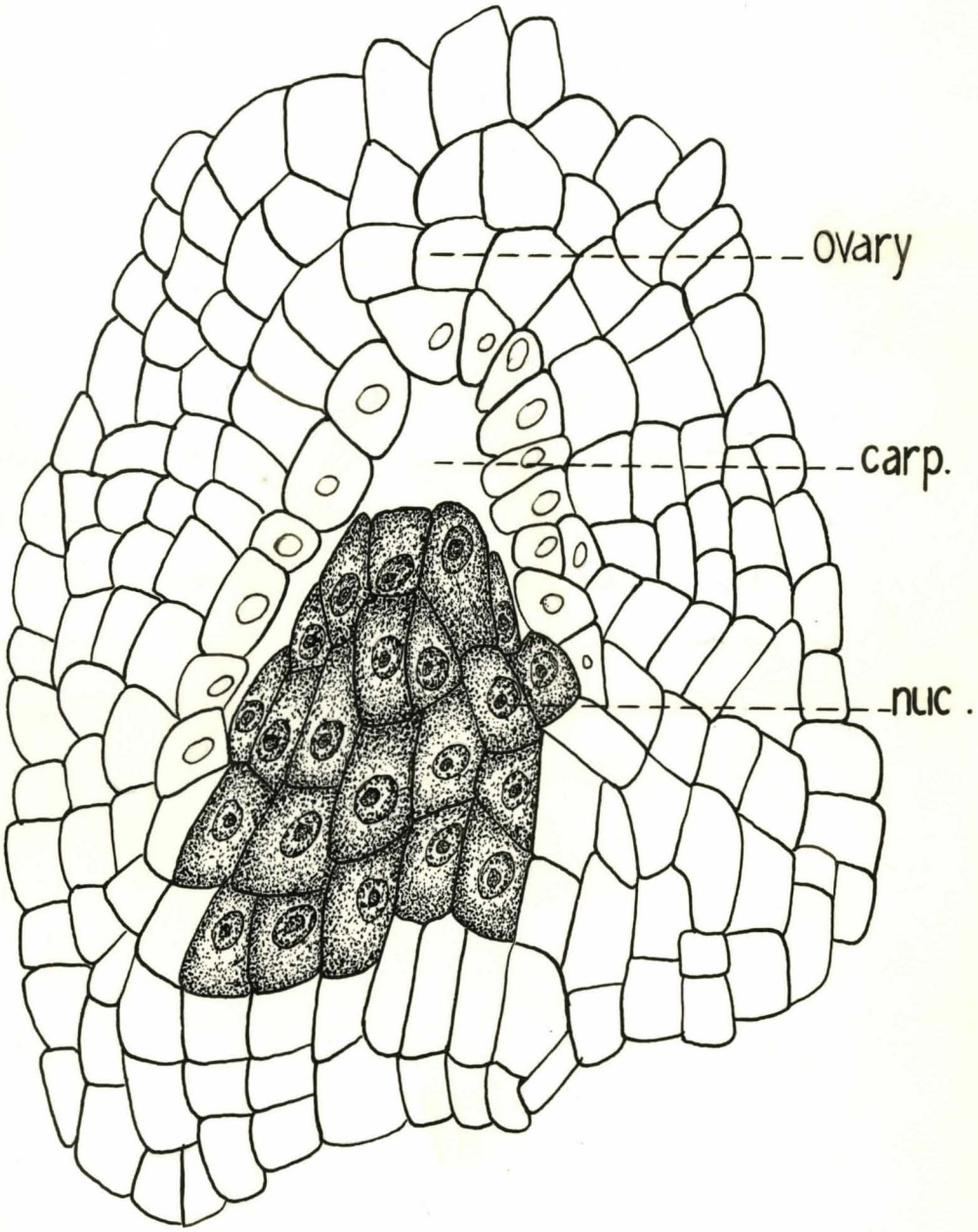

PLATE II

PLATE III

Early Development of the Integument

PLATE III

Camera-lucida drawing of longitudinal section of the developing ovule of a bud 2.81 mm. long, (collected May 28) showing the organization of cells of the nucellus about the archesporial cell. This cell which is deeply embedded in the nucellus is difficult to distinguish until after it has divided. The two layers of the inner integument are beginning to form. 1102 diameters.

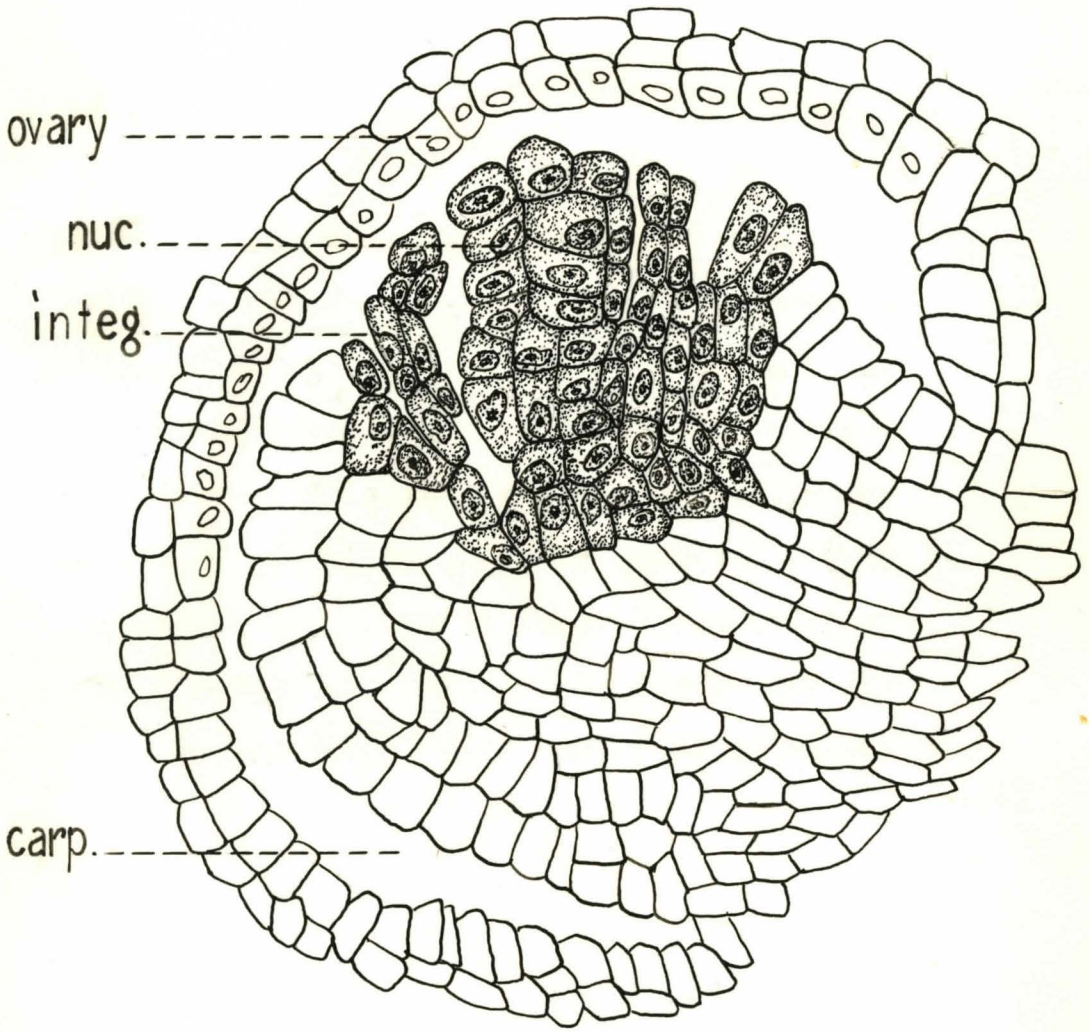

PLATE III

PLATE IV

Formation of a Tetrad of Megaspores

PLATE IV

Camera-lucida drawing of a linear row of four megaspores. The four megaspores in the ovule of a flower 4.24 mm. long (collected June 2) are the result of two successive divisions of the archesporial cell. The tetrad shows an increase in the size of the chalazal functional spore of the tetrad and an increase in the size of its nucleus before it divides. The tetrad is deeply embedded in the nucellus and the inner integument has developed to a level even with the apex of the nucellus. The inner integument of two layers, except at the base where it has three layers of cells grows upward about the apex of the nucellus. An outer integument of three layers of cells develops more rapidly on the side away from the placenta. 750 diameters.

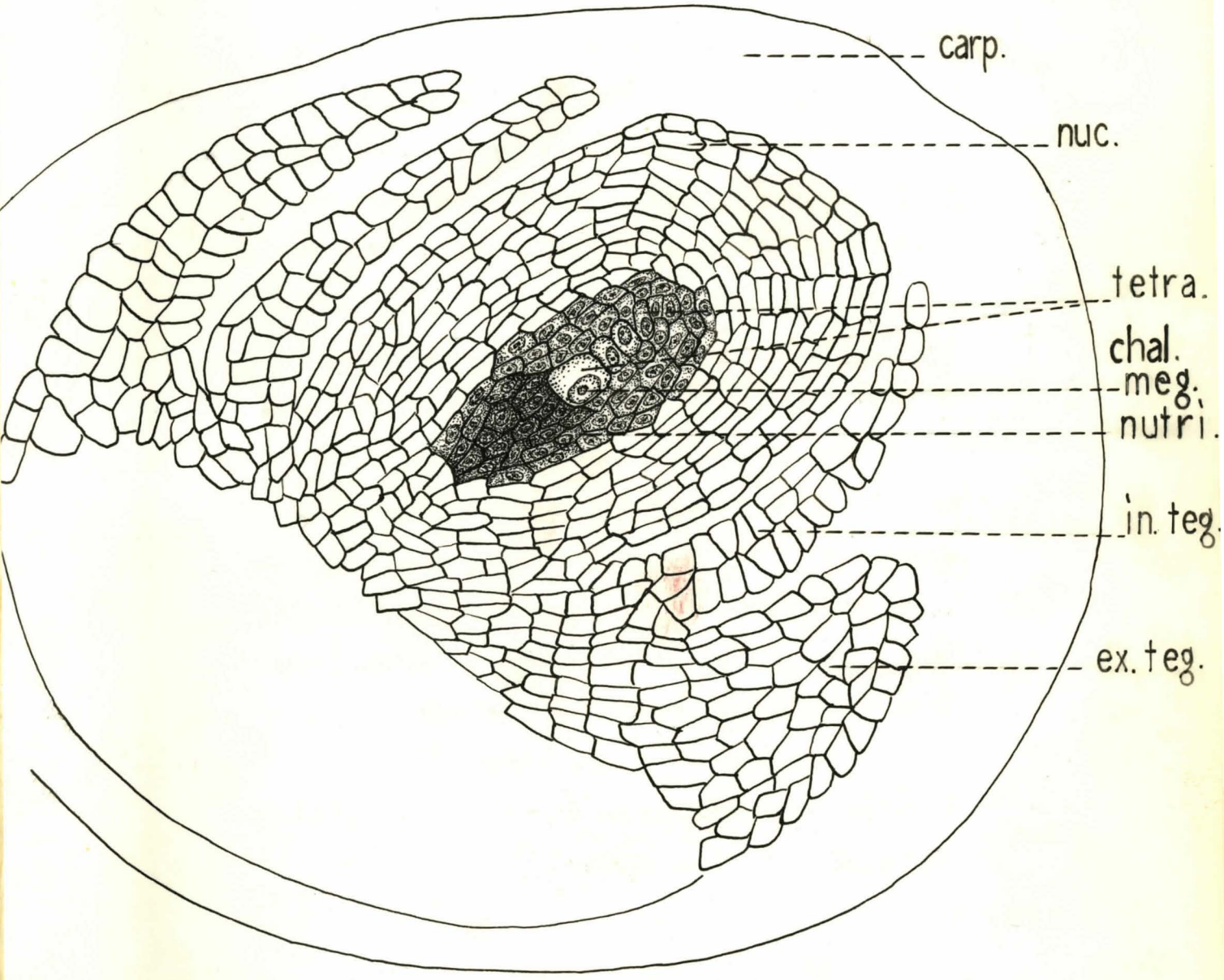

PLATE IV.

PLATE V

Longitudinal Section of an Entire Ovary

PLATE V

Camera-lucida drawing of longitudinal section through the ovary of a flower 4.24 mm. (collected June 2), showing the anatropous ovule, the growth of the integument over the micropylar end of the ovule, and the deeply embedded megagametophyte. The main vascular strand of the ovary extends into the funiculus toward the chalazal end of the megagametophyte. 485 diameters.

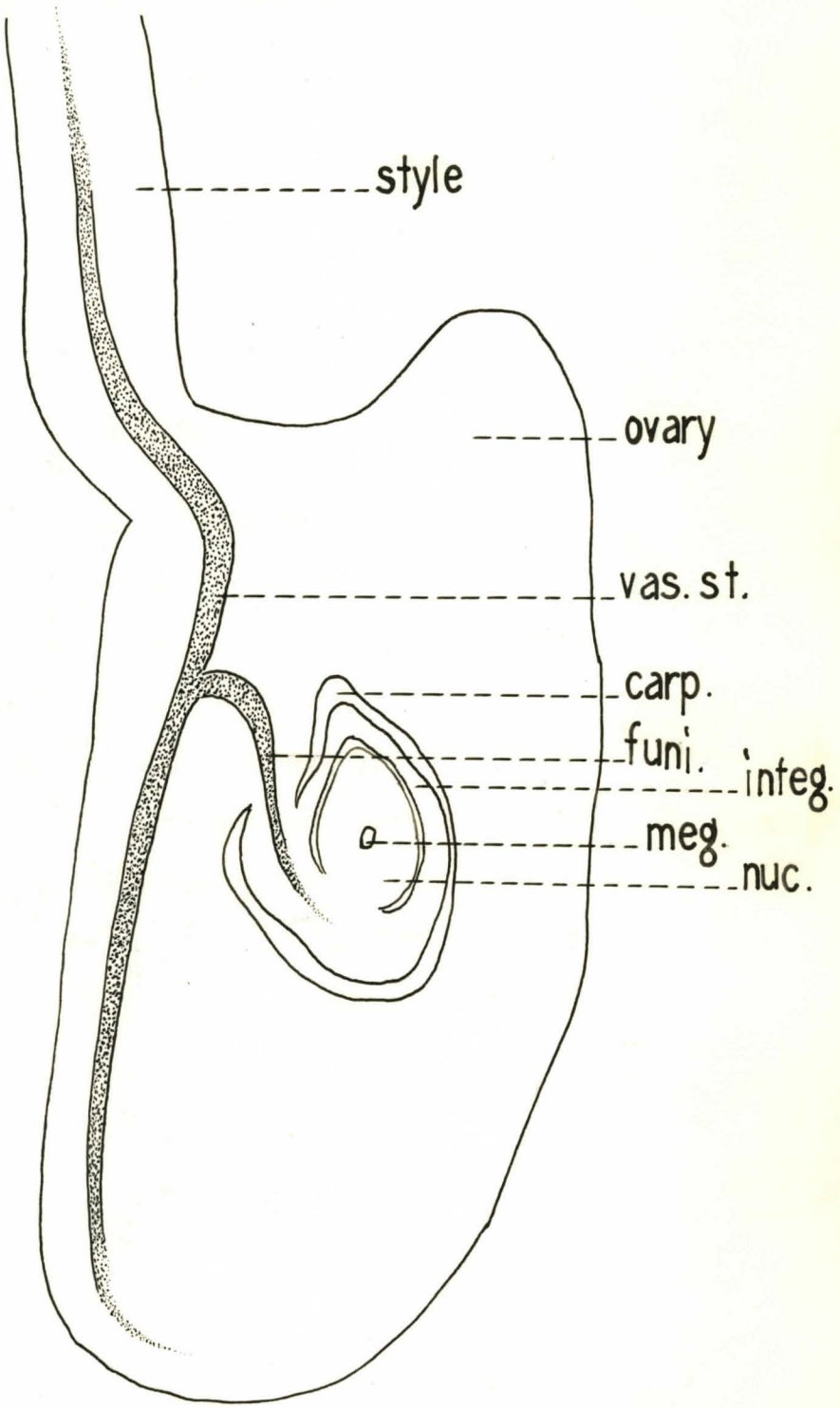

PLATE V.

PLATE VI

Development of the Chalazal Megaspore

PLATE VI

Camera-lucida drawing showing the development of the chalazal megaspore. In an ovule of a flower 4.24mm. long (collected June 2), the linear tetrad of megaspores shows a great increase in size of the functional chalazal megaspore and first division of its nucleus. The three persisting megaspores at the micropylar end disintegrate as the chalazal megaspore increases in size. A group of nutritive cells having dense cytoplasmic content are found about the chalazal end of the two-nucleate megagametophyte. 2000 diameters.

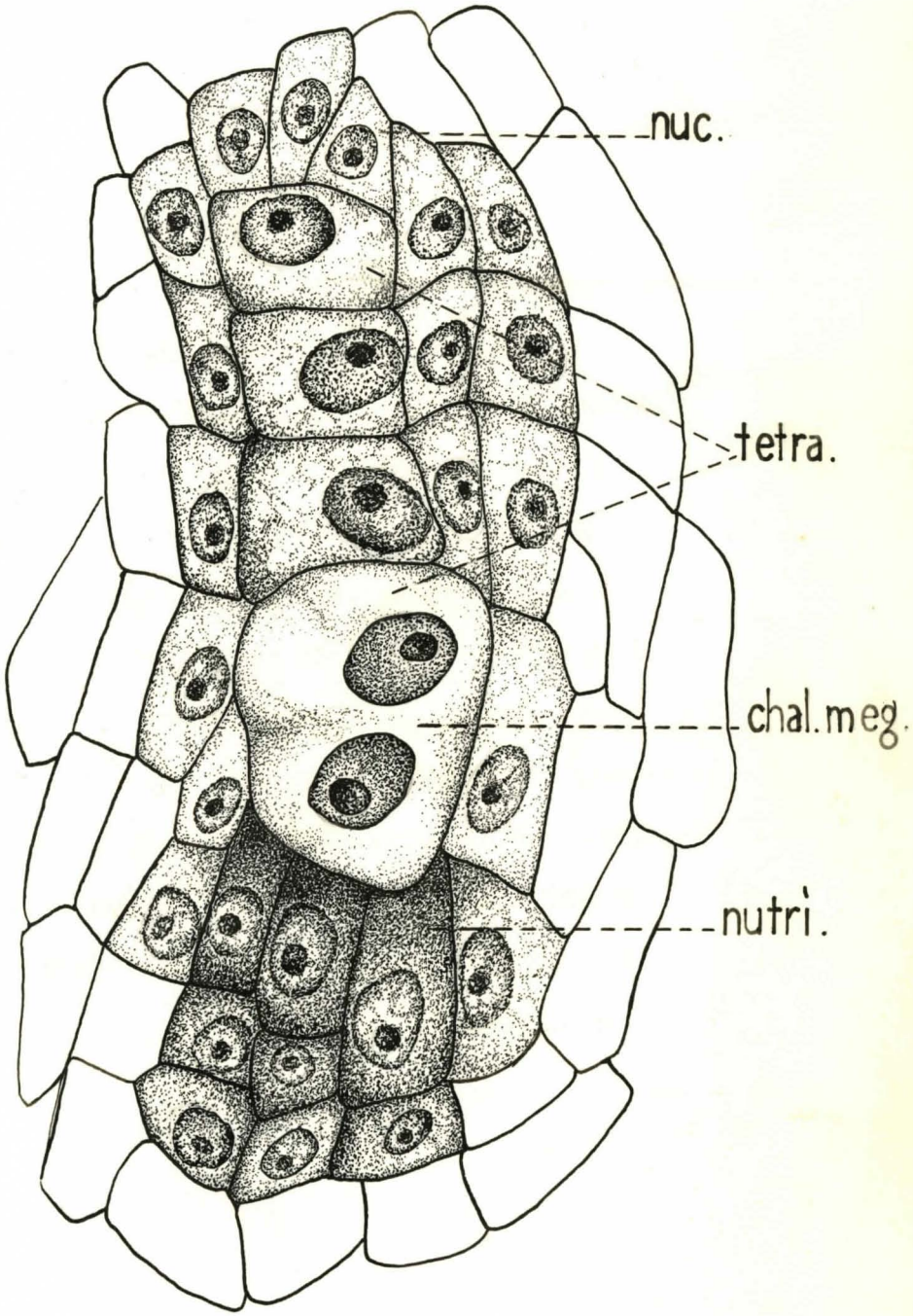

PLATE VI.

PLATE VII

Two-nucleate Embryo Sac

PLATE VII

Camera-lucida drawing of two-nucleate embryo sac in an ovule of a fruit 2.8 mm. long (collected June 5). The two nuclei resulting from the first mitotic division of the nucleus of the functional chalazal megaspore migrate apart, one going to the micropylar end and the other toward the chalazal end. The diameter of the megagametophyte has become greatly extended. A large vacuole forms in the mid-portion of the cell. 324 diameters.

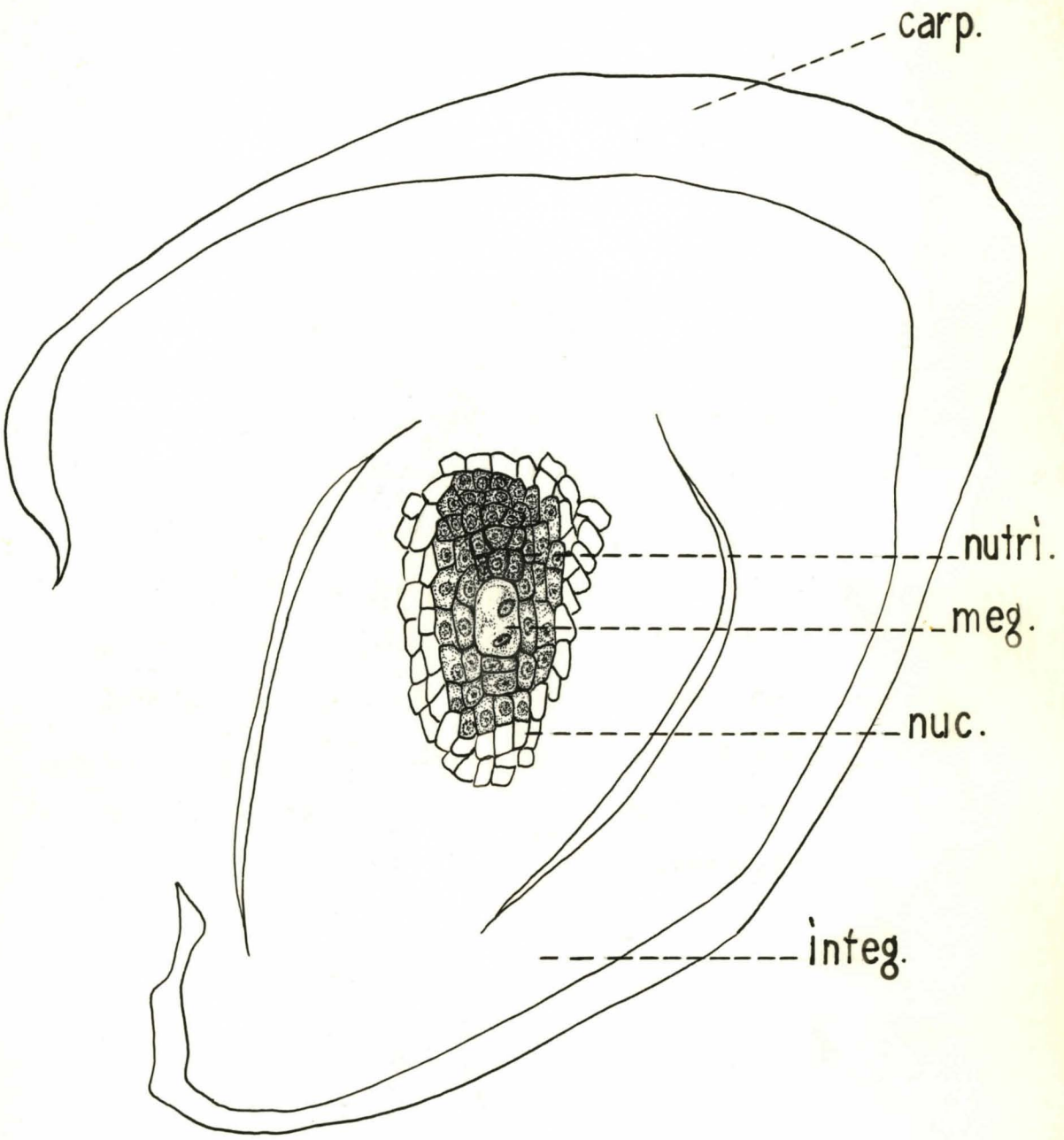

PLATE VII

PLATE VIII

Two-nucleate Embryo Sac

PLATE VIII

Camera-lucida drawing of the enlargement of the two-nucleate megagametophyte shown in PLATE VII. The two nuclei migrate apart and lie in peripheral layer of cytoplasm, one in the micropylar end and the other in the chalazal end of the embryo sac. A vacuole exists in the mid-portion of the cell. Deeply stained nutritive cells are found at the chalazal end of the embryo sac. The cells of the nucellus adjacent to the embryo sac have become flattened, elongated with the loss of nuclei, and show signs of being absorbed by the embryo sac. 2352 diameters.

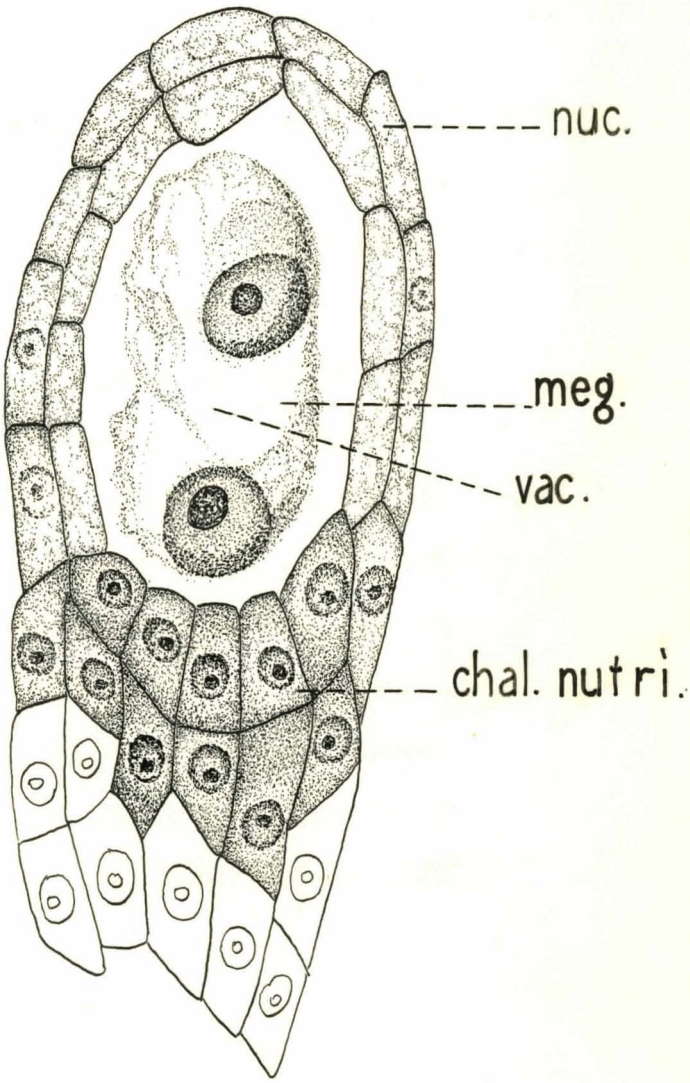

PLATE VIII

PLATE IX

Eight-nucleate Megagametophyte Stage

PLATE IX

Camera-lucida drawing of an ovule of a fruit 2.8 mm. long (collected June 5) showing the micropylar region in the eight-nucleate embryo sac stage. The four nuclei which lie in the peripheral layer of cytoplasm in the micropylar region of the embryo sac are the result of the mitotic division of the two daughter nuclei in the micropylar region. One of these, the polar nucleus migrates toward the center of the embryo sac. The embryo sac shows a greater increase in diameter in the micropylar region. 1602 diameters.

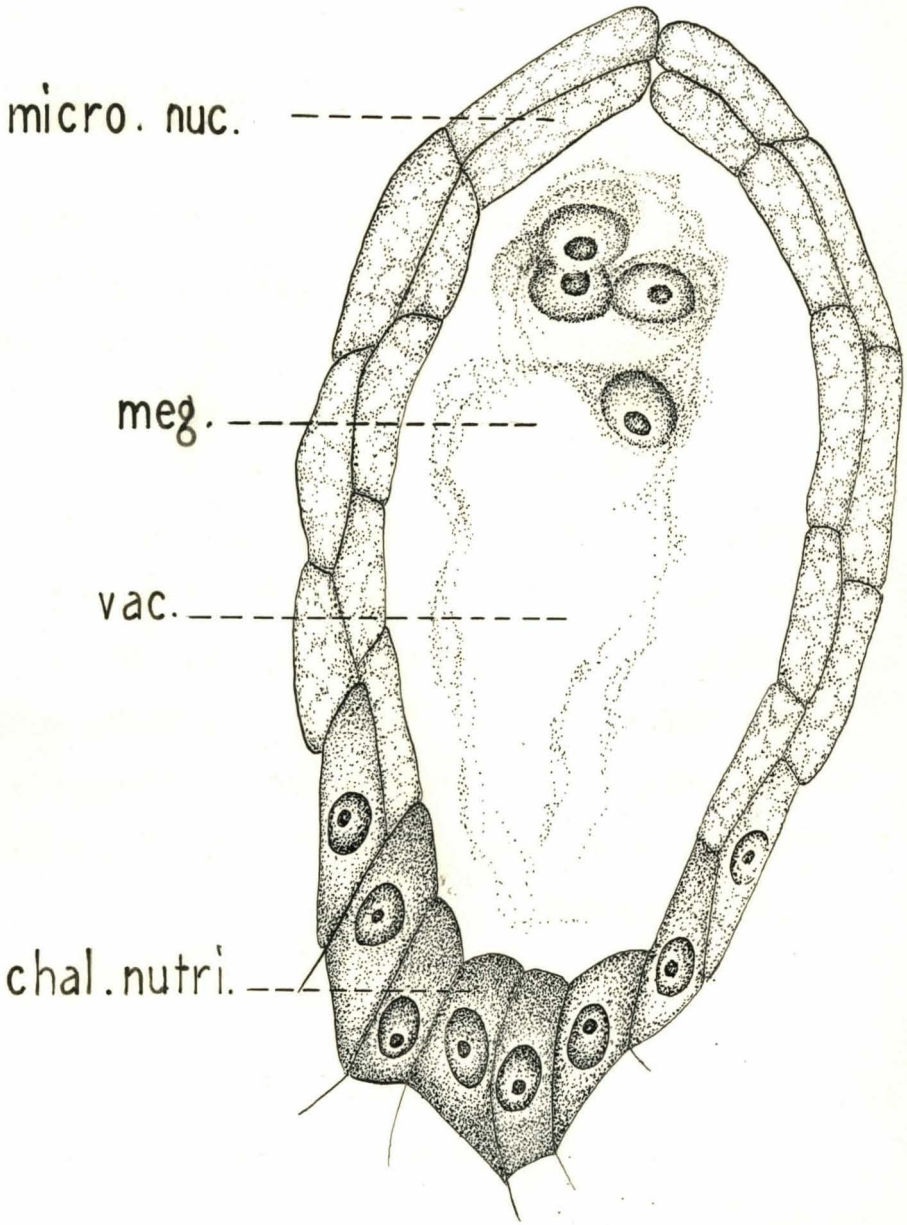

PLATE IX

PLATE X

Mature Megagametophyte

PLATE X

Camera-lucida drawing of a longitudinal section through an ovule with a seven-celled eight-nucleate embryo sac, in a fruit 4.6 mm. (collected June 8). The egg apparatus in the micropylar end consists of the egg cell and two synergids. The micropylar ends of the synergids elongate and extend toward the micropyle. The two polar nuclei devoid of a limiting membrane lie in contact with one another in the center of the embryo sac and form a two-nucleate endosperm cell. Three uninucleate antipodal cells are found in the chalazal end of the embryo sac which is still deeply embedded in the nucellus. 439 diameters.

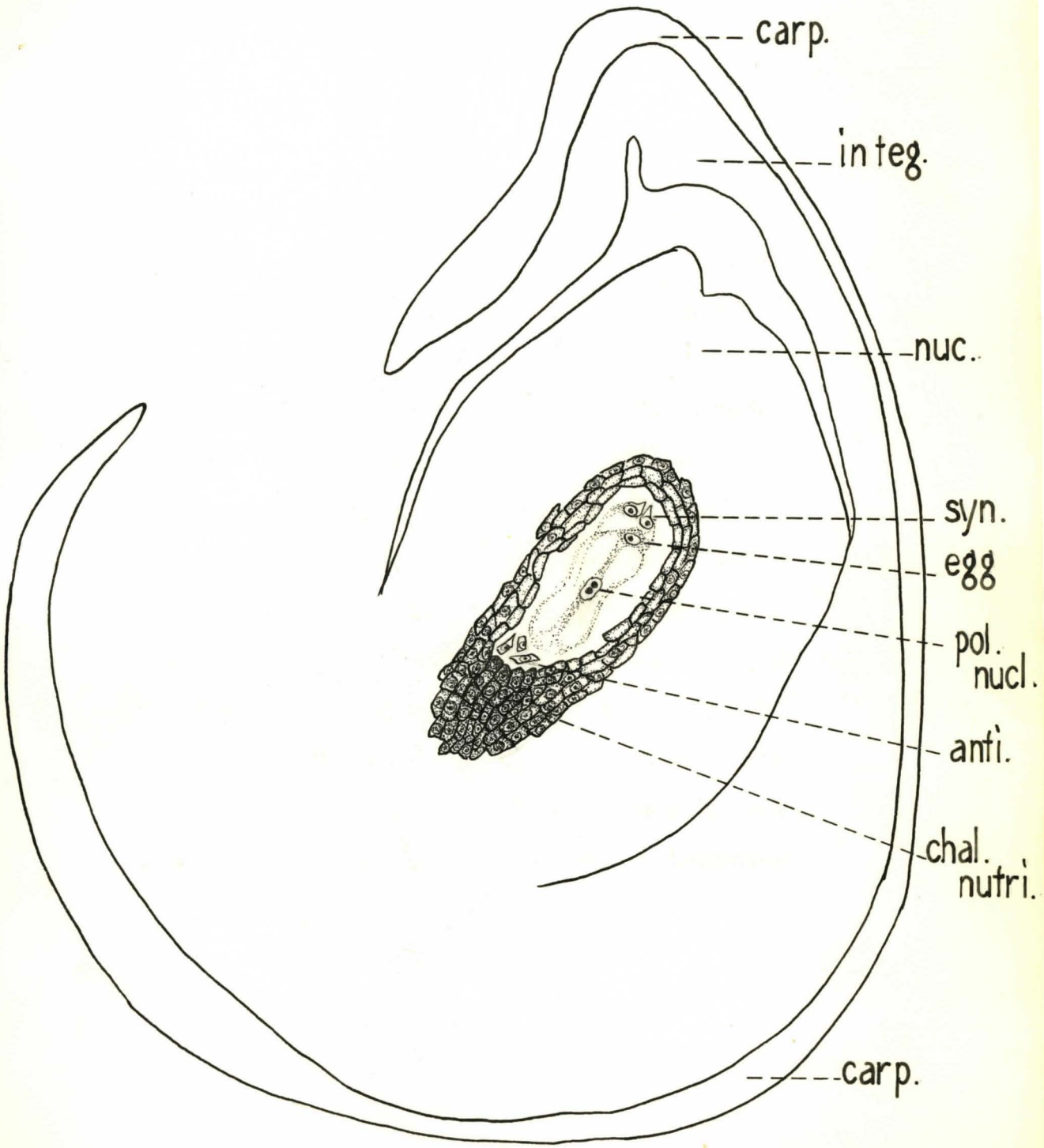

PLATE X

PLATE XI

Enlargement of Mature Megagametophyte

PLATE XI

Camera-lucida drawing of an enlargement of the mature megagametophyte shown in PLATE X. The eight-nucleate mature megagametophyte consists of three uninucleate antipodals separated from the remainder of the embryo sac, a two-nucleate endosperm cell in the center, a large egg nucleus and two synergids with smaller nuclei in the micropylar region. 2588 diameters.

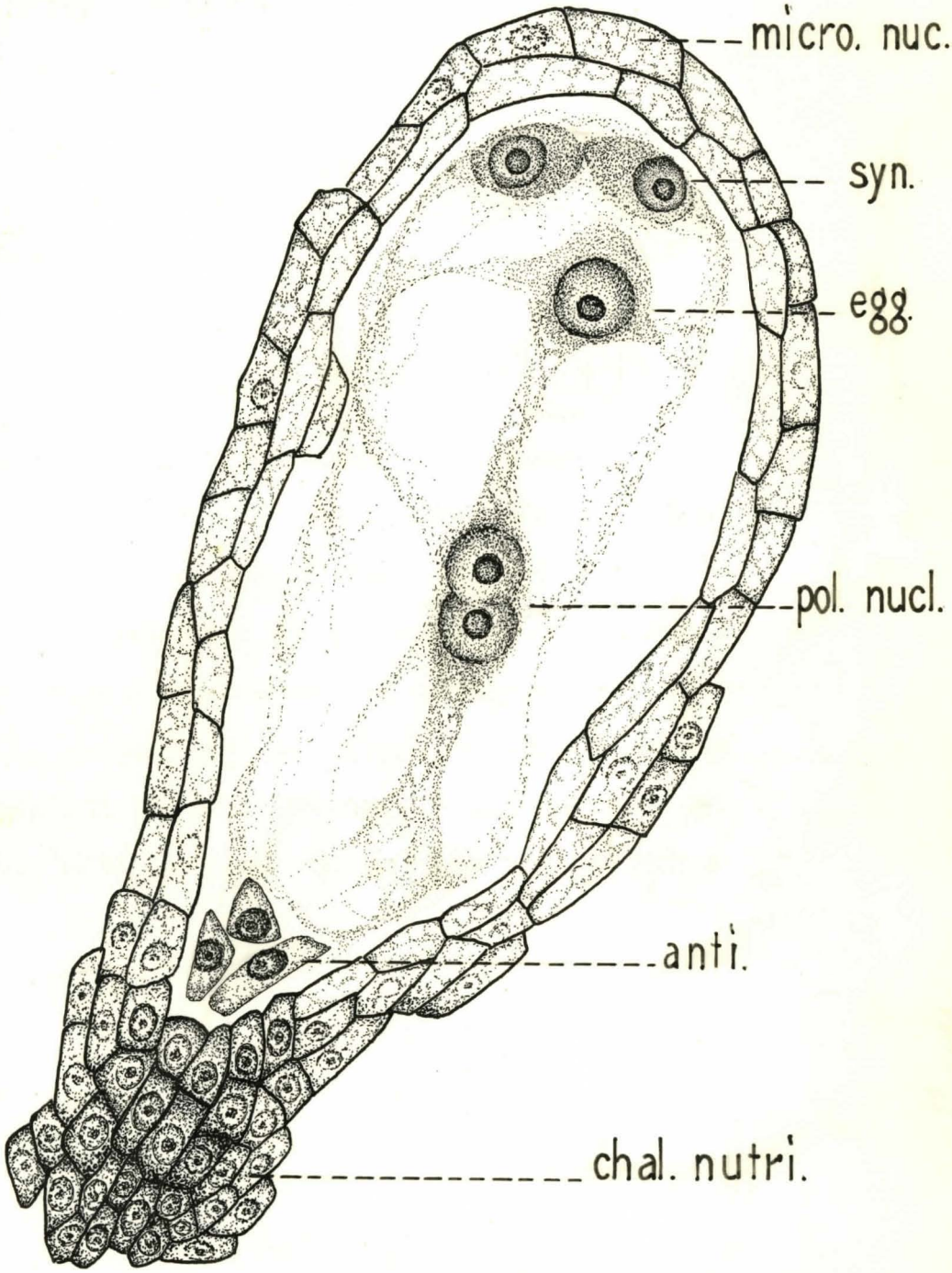

PLATE XI

PLATE XII

Formation of the Primary Endosperm Cell

PLATE XII

Camera-lucida drawing of embryo sac of ovule of a fruit 4.6 mm. long (collected June 8) showing the primary endosperm cell. The two polar nuclei have fused after cell formation. The synergids have become separated from the remainder of the embryo sac and are in stages of disintegration. The antipodals persist at this stage of development. 1838 diameters.

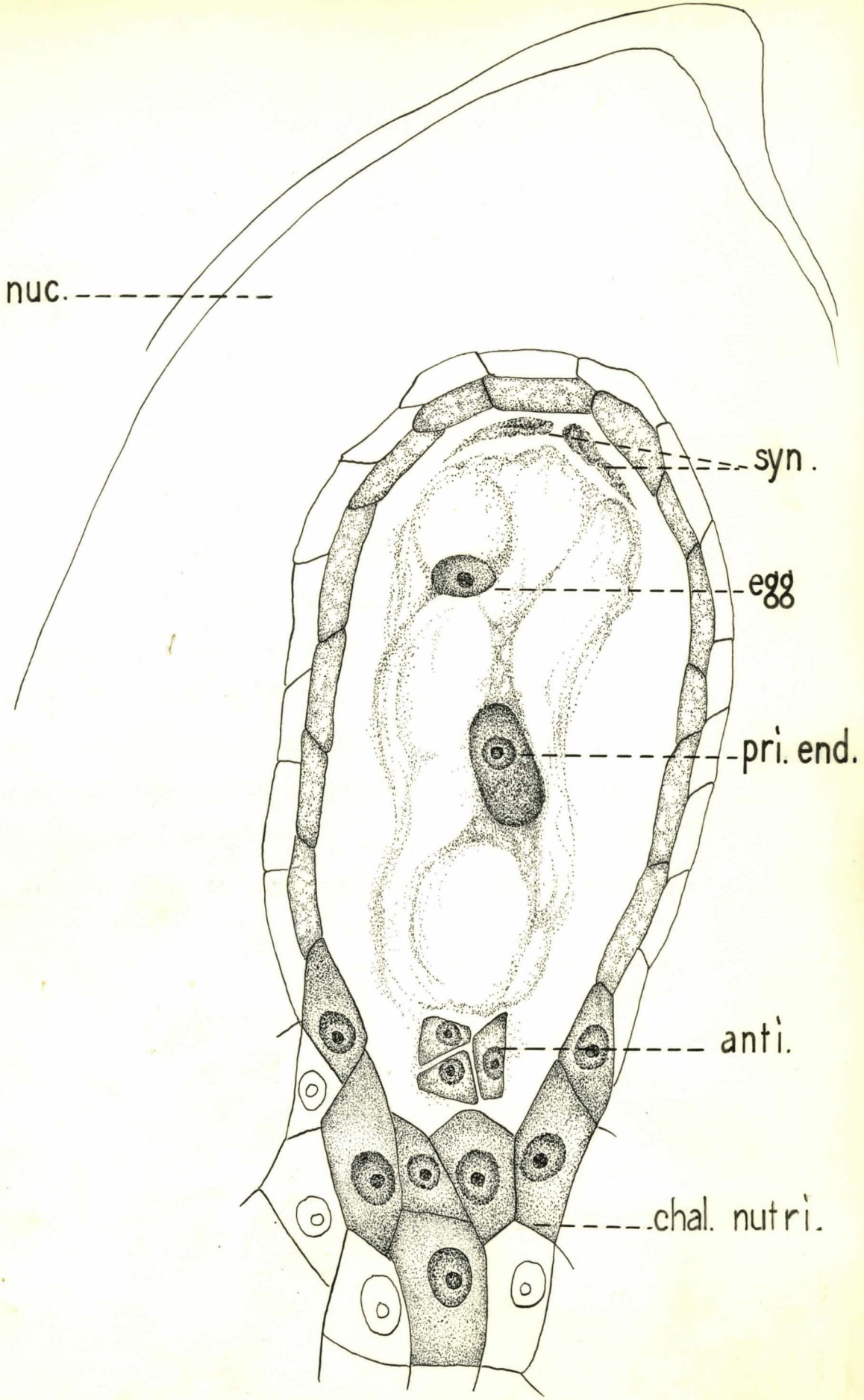

PLATE XII